

Invasive earthworm species and nitrogen cycling in remnant forest patches

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Abstract

Invasive non-native earthworms in forested areas of the northeastern United States are of concern since they have the potential to greatly change the nutrient dynamics of these ecosystems. Urban landscapes are particularly susceptible to non-native species invasions. In this study, we assessed earthworm communities and nitrogen transformations rates in urban and rural forest patches of the Greater Baltimore Metropolitan area, USA. We expected to observe a mixture of native and non-native species at the sites because the region has never been glaciated. The fauna was dominated by European lumbricids. Density and biomass varied between 5 and 288 ind m⁻² and 5.2 and 144.0 g m⁻², respectively, with urban forests having higher abundances than rural forests. In laboratory incubations, urban forest soils had higher potential N-transformation rates. Both N-mineralization and nitrification rates were positively correlated with soil pH. However, controls on earthworm communities and N-cycling are complex in the Baltimore region, because parent material and soil type also change along the urban–rural gradient. Further studies will separate out land use and inherent soil controls on earthworm populations and N-transformation rates.
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1. Introduction

The expansion of urban areas worldwide has resulted in elevated local extinction rates (Marzluff, 2001; McKinney, 2002). Urban areas are also epicenters of many non-native species introductions (Steinberg et al., 1997; McKinney, 2002). The combination of native

species extinctions and the invasion of urban adapted non-native species have resulted in a pattern where native species decrease from outlying rural areas to urban centers, while non-native species increase (Blair, 2001). Whether native species are displaced or out competed by non-native invaders is an open question in ecology (Curry, 1998; Mack et al., 2000). Preliminary investigations of birds and flying insects suggest that in the case of species responses to urban gradients the pattern expressed is from the loss of habitat rather than from competitive interactions between native and non-native species (Blair, 2001).

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The history of earthworm assemblages in the Mid-Atlantic region is complex, and difficult to reconstruct, because it was shaped by a variety of geological, climatological and anthropogenic factors. Unlike the northern part of North America, Maryland was never covered with ice. However, the vegetation was very different from the present one during the last glacial maximum. Deciduous and conifer forests were replaced by more open conifer woodlands with cooler climate species of pines and spruce as dominating components (Delcourt and Delcourt, 1987; Williams et al., 2004). Although this vegetation shift did not necessarily result in elimination of native species as in the glaciated areas (Michaelsen, 1903; Gates, 1966, 1976; Reynolds, 1994b; James, 1995), it still might have affected their distribution and abundance.

More recently, human land use practices profoundly changed vegetation, soil and its biota. Prior to European settlement, 95% of Maryland was covered by forests (Besley, 1916). By the late 1800s, the majority of the land was used as cropland or pastures (Schneider, 1996). Agricultural practices present such a major disturbance for native earthworms (James and Hendrix, 2004) that even after agricultural abandonment native species may be unable to repopulate secondary forests. Agriculture along with urbanization also greatly enhances exotic earthworm invasion.

In glaciated areas of the northeastern United States, studies have shown that urban areas are important foci of non-native earthworm introductions, especially Asian species from the genus *Amyntas*, which appear to be expanding towards outlying forested areas (Steinberg et al., 1997; Groffman and Bohlen, 1999). These findings support the hypothesis that urban landscapes are particularly susceptible to non-native species invasions (Blair, 2001). Steinberg et al. (1997) suggested that the occurrence of non-native earthworm species in urban forests may be attributable to the proximity of these forests to highly maintained landscapes such as gardens, lawns, and refuse sites, which often maintain high densities of invasive earthworm species. Moreover, urban forest habitats may sustain higher earthworm productivity and activity than surrounding forested areas due to the heat island effect (Brazel et al., 2000) and increased N-deposition (Lovett et al., 2000).

The presence of invasive non-native earthworms in forested areas of the northeastern United States is of concern since earthworms have the potential to greatly change the nutrient dynamics of forest ecosystems (Alban and Berry, 1994; Blair et al., 1995; Groffman and Bohlen, 1999; Haimi, 1995; Hendrix and Bohlen,

2002). The ability of earthworms to stimulate N cycle processes in forest soils is of particular interest (Haimi and Huhta, 1990; Haimi and Boucelham, 1991; Robinson et al., 1992; Scheu and Parkinson, 1994; Steinberg et al., 1997; Burtelow et al., 1998) and is linked to acceleration of decomposition and the formation of earthworm casts, which can function as “hotspots” of microbial activity and nitrogen cycling (Lunt and Jacobson, 1944; Parle, 1963; Lavelle and Martin, 1992; Zhu and Carreiro, 1999). Earthworm invasion of previously uncolonized forest soils results in marked reductions in soil C:N ratios (Bohlen et al., 2004b), which has been shown to decrease immobilization and increase nitrification. Nitrification, which can foster mobilization and leaching of N and other nutrients from the forest floor, appears to be particularly susceptible to stimulation by earthworms (Parle, 1963; Steinberg et al., 1997; Zhu and Carreiro, 1999).

For this study, we measured earthworm populations and N-transformation rates in forest patches embedded within urban and rural landscapes in the Baltimore metropolitan area. The Baltimore region was not glaciated and therefore native earthworm species should have been present in the landscape prior to urbanization. Therefore, unlike the studies in glaciated areas of the northeastern United States (e.g., Steinberg et al., 1997) we were able to investigate the effect of urban land-use change not only on introduced European and Asian earthworm species but also on local populations of native species. We expected that densities and biomass of non-native earthworm species would be higher in urban than in rural forest patches, while native species would exhibit the opposite pattern. We also expected that N-transformation rates would be positively correlated with non-native species densities and biomass.

2. Methods

2.1. Study area and design

The study area was located in Baltimore City and County in northeastern Maryland, USA. The Baltimore metropolitan area has hot humid summers and cold winters with average annual air temperatures ranging from 14.5 °C in Baltimore City to 12.8 °C in the surrounding area (NOAA, 2000). This difference in air temperature between the city and surrounding areas is attributed to the heat island effect associated with Baltimore City (Brazel et al., 2000). Precipitation is distributed relatively evenly throughout the year for the entire study area and ranges from an annual average of

107.5 cm in Baltimore City to 104 cm in the surrounding metropolitan area (NRCS, 1998). Baltimore County and the northern half of Baltimore City lie within the Piedmont Plateau. Most of the city and county are characterized by nearly level to gently rolling uplands, dissected by narrow stream valleys. The Piedmont Plateau in the Baltimore metropolitan area is underlain by schist, gneiss, gabbro, and other highly metamorphosed sedimentary and igneous rocks.

Potential study sites were selected using aerial photographs, topographic maps, and prior knowledge of the Baltimore metropolitan area. In order to reduce potential sources of variation, the following criteria were used to screen potential stands prior to inclusion in the study: (1) size ≥ 2 ha, (2) overstory dominated by white oak (*Quercus alba*) and tulip poplar (*Liriodendron tulipifera*), (3) slopes $< 15\%$, and (4) an age of 60+ years with no visual signs of recent human disturbance.

Once selected, each stand was classified as urban, suburban, or rural based on distance from the city center and type of development in the surrounding area. Three urban stands (Cylburn Arboretum, Hillsdale Park, and Leakin Park), were located within 9 km from the city center and surrounded by high-density residential and commercial structures. Two suburban stands (Mount Pleasant Park and Pimlico Park) were located at least 10 km from the city center and surrounded by mid- to low-density residential and commercial structures. Three rural stands (Liberty and Loch Raven Reservoirs and Oregon Ridge Park) were located > 19 km from the city center and largely surrounded by a mix of agricultural land and low-density residential structures (Table 1). Every attempt was made to select sites on

similar soil types, but due to unavoidable differences in surface geology between the City and County of Baltimore, not all of the plots occur on similar soils. The LP and CA stands occur on Legore loam and the HP and PP stands on Jackland silt loam soil series. Legore soils are very deep, well drained soils that overlie semibasic and mixed basic and acidic rock on moderately sloping ridgetops and side slopes. Jackland soils are moderately well drained and somewhat poorly drained soils on upland flats and footslopes of the Piedmont Plateau. The MP and rural stands occur primarily on Manor loam soil series. These soils formed from micaceous parent material and are somewhat excessively drained soil on side slopes of the Piedmont Plateau (Reybold and Matthews, 1976; Levin and Griffin, 1998).

In each stand, three 0.04 ha circular plots were randomly established for soil and earthworm sampling (total of 24 plots). Plots were located on level topography and in undisturbed locations. Three earthworm samples were taken from each plot (see below). For soil analysis and microbial incubation, two soil cores (5 cm diameter, 10 cm deep) were taken directly adjacent to the earthworm quadrat. The litter layer (Oi) was removed from the soil surface prior to removing the double cores, which were later composited into one sample. Each composite sample was placed in separate Whirl-pak bags, and stored on ice and later refrigerated at 4 °C before preparation (less than 7 days). Soil temperature and leaf litter thickness were also determined on each plot. Overall nine earthworm and soil samples were taken per forest stand. Sampling took place from 9 to 13 November 2002. Earthworms are very active during this time of the year due to high

Table 1
Locations and site properties of the forest stands

Site	Size (ha)	Elevation (m)	Distance from urban core (km)	Soil series
Urban				
Cylburn	47.3	120	6.5	Legore loam
Hillsdale	13.8	111	9.0	Jackland silt loam
Leakin Park	176.2	90	8.0	Legore loam, Jackland silt loam
Rural				
Liberty Reservoir	64.4	159	29.0	Manor loam
Loch Raven Reservoir	128.7	138	18.5	Manor loam
Oregon Ridge	346.5	153	23.0	Manor loam, Glenelg channery loam
Suburban				
Mount Pleasant	12.8	75	10.5	Manor loam
Pimlico	2.0	126	10.0	Jackland silt loam

precipitation, and availability of freshly fallen leaf litter.

2.2. Earthworm sampling

Earthworms were extracted from 25 cm × 25 cm quadrants using a mild (0.2%) formaldehyde solution (Raw, 1959). Three samples per plot (a total of nine samples per forest) were taken. The animals were killed in 75% ethanol, fixed in 4% formalin for several days and preserved in 75% ethanol. Adult earthworms were later identified to species, juveniles to the next taxonomic level. We were concerned that the earthworm extraction method may undersample native endogeic species, such as *Diplocardia* (Lee, 1985; James, 1990). To verify the extraction results, we extensively dug in the area to make sure that the native *Diplocardia* or other genera were not overlooked. The taxonomy and nomenclature of *Octolasion lacteum* and *Aporrectodea caliginosa* are controversial. We followed the system of Csuzdi and Zicsi (2003), where they discuss these issues in detail. To determine biomass the weight of preserved earthworms were multiplied using a species dependent correction factor (Zicsi, 1974). At the same time, earthworms were extracted leaf litter depth and soil temperature (0–10 cm depth) were determined at 12 randomly selected points in each plot. Soil moisture, conductivity, and pH were later determined in the laboratory (see below).

2.3. Nitrogen cycle processes

Soil samples were sieved to remove material greater than 6.4 mm (0.25 in.), while preserving crumb and granular soil structure. Soil moisture content was

determined by drying at 105 °C for 48 h. Soil organic matter content was determined by loss on ignition at 450 °C for 4 h. To determine soil pH approximately 10 g (dry weight) soil was mixed with deionized water at 1:2 ratio, shaken vigorously for 2 min, and allowed to settle. Soil pH and conductivity were measured using a Barnart 20 digital pH/mV/ORP meter kit 559–3800.

Potential N-mineralization and nitrification rates were measured from the accumulation of NO_3^- plus NH_4^+ and NO_3^- alone during a 21-day aerobic incubation at 17 °C under field moisture conditions (Robertson et al., 1999). Field moisture was used since soil moisture measurements were similar among all sites (Table 2). Subsamples were placed in glass 40 mL jars; each jar contained approximately 10 g dry weight soil. Two subsamples of each sample were extracted immediately with 50 mL of 2 N potassium chloride. After settling for 24 h, the potassium chloride extracts and method blanks were filtered to remove suspended and floating material. The remaining subsamples were covered with plastic wrap to minimize water loss but allow gas exchange. After the incubation period, samples were removed and extracted with 50 mL potassium chloride. The filtrate was analyzed by colorimetric analysis with a Perstorp Flow Solution Analyzer.

Potential net nitrification rates were calculated as the change in extractable NO_3^- -N concentrations during incubation. Potential net N-mineralization was the change in the sum of NO_3^- -N and NH_4^+ -N concentrations during incubation. Denitrification and ammonium volatilization were assumed to be negligible during the incubation period. Data on potential net N-mineralization and nitrification are reported on a soil dry weight (SDW) and ash free weight (AFW) basis. Reporting

Table 2
Soil properties in the forest stands (factors reflect conditions at the time of sampling)

Site	Organic matter (%)	pH	Conductivity (mV)	Moisture (%)	Leaf litter thickness (cm)
Urban					
Cylburn	7.5	5.3	121	27	2.5
Hillsdale	6.7	4.7	139	25	2.8
Leakin Park	6.8	5.3	134	22	3.4
Rural					
Liberty Reservoir	6.6	5.0	125	23	1.9
Loch Raven Reservoir	10.8	4.3	161	30	3.1
Oregon Ridge	9.3	4.4	157	26	2.4
Suburban					
Mount Pleasant	10.8	4.2	168	24	2.8
Pimlico	9.6	5.0	121	27	3.3

Table 3

List of earthworm species and their relative abundance in the sample

	Frequency	Percentage in total sample by number abundance by number	Percentage in total sample by weight
<i>Aporrectodea caliginosa</i> (Savigny, 1826)	3U; 1S	9.3	8.6
<i>Aporrectodea limicola</i> (Michaelsen, 1890)	3U; 1S	26.7	10.1
<i>Aporrectodea</i> sp. juv.	3U; 1S	12.4	2.1
<i>Lumbricus friendi</i> (Cognetti, 1904)	1S	0.5	1.4
<i>Lumbricus terrestris</i> (Linnaeus, 1758)	3U; 2R; 2S	8.4	48.3
<i>Lumbricus</i> sp. juv.	3U; 3R; 2S	37.8	27.0
<i>Octolasion lacteum</i> (Örley, 1881)	2U; 1R; 1S	4.0	1.5
<i>Diplocardia patuxentis</i> (Csuzdi and Szlavecz, 2002)	1R	0.2	0.1
<i>Amyntas hilgendorfi</i> (Michaelsen, 1892)	1R	0.4	0.9

Frequency indicates the number of forest stands the species was found (U: urban; R: rural; S: suburban).

data on N-mineralization on an AFW basis takes into consideration any variation that may occur among sites in the concentration of soil organic matter.

2.4. Statistical analysis

A one-way ANOVA using a mixed model (Proc MIXED, SAS Version 8.0) was performed to determine differences by land use in net N-mineralization and nitrification rates, earthworm density and biomass, and the soil characteristics measured. Since the number of plots sampled varied for each land-use type, Hochberg's method for unequal sample sizes (SAS Institute, Cary, NC) was used to determine significant differences between means. Spearman rank correlations were used to explore relationships between N-transformation, earthworm biomass and density, and soil characteristics among land use types ($n = 3, 2$, and 3 for urban, suburban and rural types, respectively) and among plots within each land use type ($n = 9, 6$, and 9 for urban, suburban, rural stands, respectively).

3. Results

3.1. Earthworms

Seven Oligochaeta species were found in our samples (Table 3). All, but one, *Diplocardia patuxentis* are non-indigenous. The recently described native *D. patuxentis* was found in only one rural location but has been collected from other forests around the Baltimore area (Csuzdi and Szlavecz, 2002). The remainder of the fauna consists of well-known, ubiquitous species, some of which are considered invasive. The majority of the earthworms were juvenile *Lumbricus* sp., and *Aporrectodea limicola* was the second most abundant species. This species is found in moist environments,

so their abundance in the upland forests is somewhat surprising. The earthworm biomass was dominated by the large, anecic *Lumbricus terrestris* and *Lumbricus* sp. juv. The other *Lumbricus* species (*L. friendi*) was recently added to the Oligochaeta list of North America. This species has been found at other localities in the Greater Baltimore area (Csuzdi and Szlavecz, 2003). Earthworm density and biomass were approximately eight and six times higher in urban than in rural stands, respectively, with the suburban stands in between (Fig. 1). However, the values were not significant at the $P = 0.05$ level due to the small sample size.

3.2. Potential N-mineralization and nitrification

Rates of N-mineralization significantly differed across land-use types on a soil dry weight (SDW) and ash-free weight (AFW) basis ($P = 0.021$ and 0.006 using ANOVA) (Fig. 2). When accounting for differences in organic matter content (AFW basis), the urban stands had up to three-fold higher N-mineralization rates than the suburban and rural stands

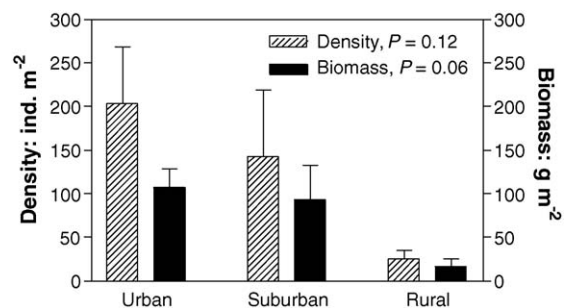


Fig. 1. Abundance of earthworm communities (mean \pm S.E.) in remnant forest patches of the Baltimore Metropolitan Region. P -values indicate results of one way ANOVA with Hochberg's method for mean separation.

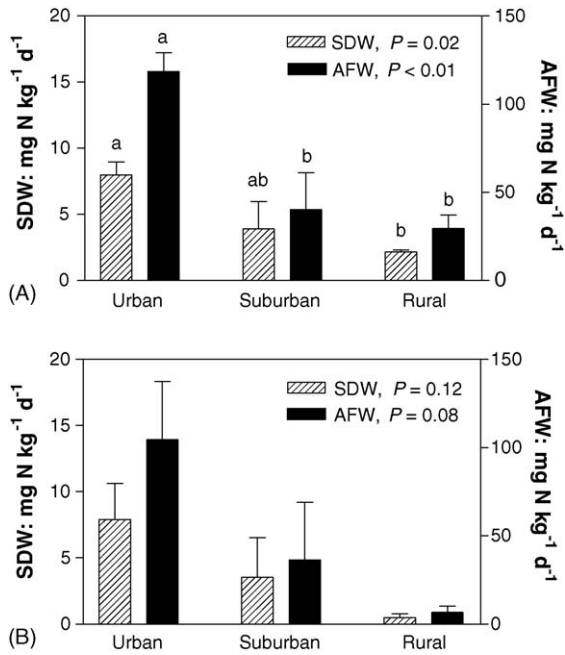


Fig. 2. Potential nitrogen mineralization (A) and nitrification rates (B) in forest soils of the Baltimore Metropolitan Region. Mean values (\pm S.E.) are given on soil dry weight (SDW) and soil organic matter (AFW) basis. *P*-values indicate results of one-way ANOVA with Hochberg's method for mean separation.

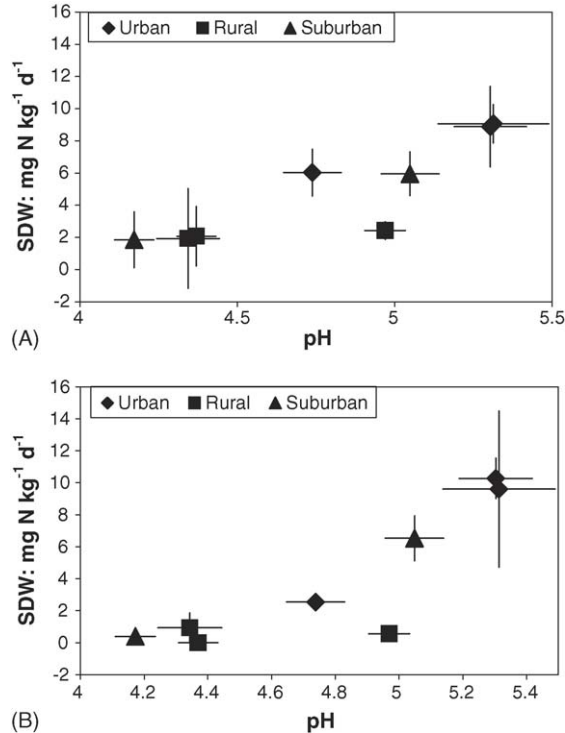


Fig. 3. Correlation between soil pH and nitrogen cycling processes: (A) potential N-mineralization; (B) potential nitrification. Mean values (\pm S.E.) are given.

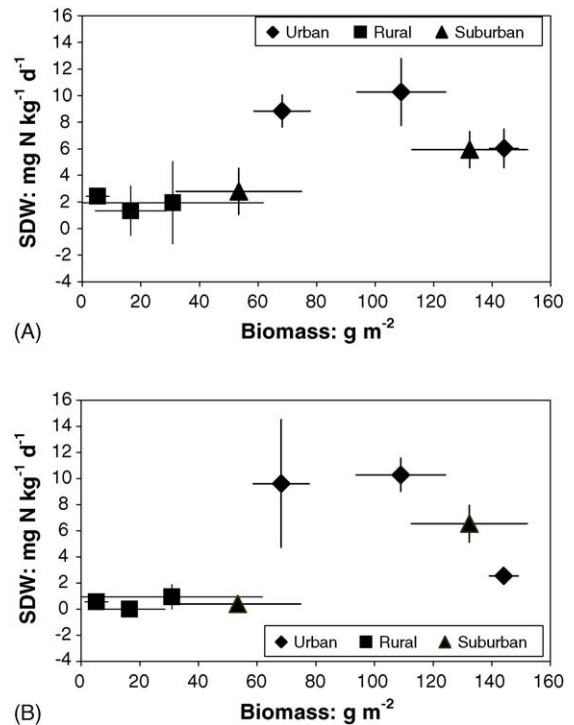


Fig. 4. Correlation between earthworm biomass and nitrogen cycling processes: (A) potential N-mineralization; (B) potential nitrification. Mean values (\pm S.E.) are given.

($P = 0.02$ and 0.008 using Hotchberg's test) (Fig. 2A). Smaller differences in N-mineralization were found among land-use types on a SDW basis with significant differences occurring between urban and rural stand means ($P = 0.022$ using Hotchberg's test) (Fig. 2A). Similar to N-mineralization, the urban stands had over four- and two-fold higher net nitrification rates than in the rural stands on an AFW and SDW basis, respectively, but these differences were not significant at $P < 0.05$ given the low power of the experimental design ($P = 0.12$ and 0.08 in the ANOVA) (Fig. 2B).

Evaluations between N-mineralization and nitrification rates and soil characteristics showed a strong positive relationship with soil pH ($r = 0.93$, $P < 0.001$ and $r = 0.83$, $P = 0.01$) using Spearman correlation (Fig. 3). There was a positive relationship between N-mineralization and nitrification and earthworm biomass but these relationships were not statistically significant at $P < 0.05$ using Spearman correlation ($r = 0.55$, $P = 0.16$ and $r = 0.64$, $P = 0.09$, respectively) (Fig. 4).

4. Discussion

Forests in the Greater Baltimore area are dominated by non-native lumbricid earthworms. The general lack

of native species across the gradient, rather than increasing from urban to rural areas suggests that their absence is not related to the presence of non-native species; we have no evidence that non-native species are outcompeting native ones. On the other hand, the high abundance and biomass of non-native species in or near the urban core support the hypothesis that urban areas can be foci for introduction and establishment of non-native species.

The species richness in our sample was relatively low, representing only a subset of the species known to occur in the area (Reynolds, 1974a). Since sampling took place late fall, *Amyntas hilgendorfi* was barely represented in the samples. This species is known to reach its peak activity in the summer and gradually disappear in the fall. Our abundance data fall within the range (0–192 ind m⁻² and 0–153 g m⁻² for total density and biomass, respectively) summarized by Satchell (1983) for a number of European oak forests. Our maximum density is higher, (288 ind m⁻² in the urban Cylburn forest), but this may be due to the large number of juveniles at this site and time of the year. Humus type rather than vegetation can be a good indicator of earthworm abundance, as was shown in a comparative synthesis by Phillipson et al. (1978). Earthworms on mor humus reach an average density of 25 ind m⁻², and an average biomass of 7.8 g m⁻². On mull values are 101 ind m⁻² and 29 g m⁻², respectively. Our abundance data in the urban (mull) and rural (mor) sites show the same pattern, but the abundances in the urban forests are higher (urban: 204 ind m⁻² and 107 g m⁻²; rural: 24 ind m⁻² and 17 g m⁻²). Since earthworms are able to transform mor humus into mull, to provide an explanation of the observed pattern the original site conditions (mull or mor), and long-term dynamics of the study sites (different opportunities for colonization) must be known.

Both N-mineralization and nitrification rates were higher in the urban than in the rural stands. These results are consistent with the New York City urban–rural gradient study (Steinberg et al., 1997; Zhu and Carreiro, 1999; Pouyat and Turechek, 2001) where exotic earthworm invasion was a dominant controller of soil N dynamics. Not all studies have found a strong earthworm effect on N storage and availability. In a comprehensive study at sugar maple dominated forests, Bohlen et al. (2004b) and Groffman et al. (2004) found that while plots invaded by exotic earthworms had higher microbial respiration rates, N-mineralization and nitrification rates were not different from control plots. Clearly, the relationship between earthworm communities and soil nutrient

cycling is complex. It involves direct and indirect interactions among many factors, such as previous land use history, vegetation and microbial community dynamics, and initial amount and quality of organic matter, all of which operate at different spatial and temporal scales (Bohlen et al., 2004a,b; Groffman et al., 2004; Lavelle et al., 2004).

Our results in Baltimore may be confounded by differences in parent material and soil type along our urban–rural gradient. The Baltimore metropolitan region straddles the fall line between the Atlantic Coastal Plain and the Piedmont Plateau, each of which have different soil types. The urban stands in this study are located on or near the fall line between the plateau and coastal plain where soils have formed in semibasic and mixed basic rock. Soils developing north of the fall line (our rural plots) tend to be more acidic. The more acidic soils might naturally be expected to support lower levels of earthworms and N-cycling. The two suburban stands illustrate the importance of this soil effect. One of the suburban stands (Pimlico) is on Jackland silt loam over basic rock, and has relatively high earthworm biomass and N-cycling, while the other (Mount Pleasant) on Manor loam, the more acidic rock types has relatively low earthworm biomass and N-cycling (Tables 1 and 2). These results suggest that controls on earthworm communities and N-cycling are more complex along the Baltimore urban–rural gradient than they were in New York and will require further analysis to separate out land use and inherent soil controls.

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